STUDIES ON THE GENETIC NATURE OF RESISTANCE TO *PUCCINIA GRAMINIS* VAR. *TRITICI* IN SIX VARIETIES OF COMMON WHEAT

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Synopsis

The mode of inheritance of resistance to stem rust was determined for six varieties of *T. vulgare.* In the case of Eureka the type of F_2 segregation obtained in crosses with susceptible varieties was influenced by temperature and by the strain used. The resistance of Eureka to the laboratory strain 103–H–2 was controlled by two independent factors, Sr6 and an incompletely dominant factor which was not temperature sensitive.

In each case a different factor conditioned the seedling resistance of Gabo to the strains 126–Anz–6, 21–Anz–2, 103–H–2 and A20. Three of these factors were also present in Charter, but only one (Sr11) in Yalta. The gene Sr11 in Gabo, Charter and Yalta was differentially transmitted in crosses between these three varieties and the susceptible Mentana and Chinese Spring, and also, apparently, in crosses with Federation and Morocco. Sr11 was closely linked with the factor for leaf rust resistance in Mentana. Another factor, Sr_{G2}, in Gabo and Charter conferred resistance to strains 103–H–2 and 111–E–2, but was ineffective against field strains.

Seedling resistance of Mentana to 21–Anz–2 was controlled by a single factor, Sr8, which, together with another factor, conferred resistance to NR–7.

Kenya 117A was found to possess three factors for seedling resistance of which one, Sr9b, also conferred field resistance, while the other two had only a modifying effect. In the seedling stage Sr9b was dominant with 222–Anz–1, 2, 4, 6 but incompletely dominant with other strains.

INTRODUCTION

The task of the plant breeder who is concerned with developing varieties of wheat resistant to *Puccinia graminis* Pers. var. *tritici* (Eriks. and E. Henn.) has been made difficult by the existence of many pathogenic strains of the parasite. Especially in recent years, the rapid spread of virulent strains of the 21 and 34 standard series has been a setback to breeders in New South Wales and Queensland, as these strains rendered susceptible the commonly used sources of resistance. All the six varieties used in this study are no longer resistant to the stem rust strains occurring in the field, while a few years ago the resistances of Eureka and Kenya 117A were still effective against most field strains.

The present study was undertaken to study the mode of inheritance of resistance in six varieties of *Triticum vulgare* to some of the new strains of stem rust, and to correlate results obtained by Australian and overseas workers, which were at variance. A special effort has been made to study the effect of minor or modifying genes as these could be of some use in future breeding work.

REVIEW OF LITERATURE

For the purpose of this review the types of resistance carried by the three varieties, Gabo, Charter and Yalta are considered together and the other varieties *seriatim.*

Eureka

In 1941 Macindoe reported that a single factor in Eureka conferred resistance at lower temperatures; this factor was non-allelic to the single factor in the varieties Charter and (Gaza × Bobin[2]), the latter being a sisterline to Gabo.

Watson and Waterhouse (1945) showed that the resistance factor in Eureka derived from Kenya W 743* C6040 was inherited independently of the single factors for resistance in Kenya W 744 C6041 and Kenya W 745 C6042. Knott and Anderson (1956) have designated this factor Sr6. Studying the mode of inheritance of resistance, they postulated that Sr6 is dominant with race 56 but recessive with race 15B. Recent work by Green *et al.* (1960), using many North American and Australian strains, indicated that Sr_{Kal} (a designation used by Australian workers for the resistance gene in Eureka) and Sr6 are the same and this was also apparent when all F_2 plants from a cross between Eureka and the isogenic Sr6 line proved resistant to races 56 and 15B. Peterson and Campbell (1953) located Sr6 on chromosome XX and this has been confirmed by other workers. The effect of temperature on the breakdown of rust resistance in varieties carrying Sr6 has been described by Green and Johnson (1954) and Forsyth (1956).

A second gene for resistance in Eureka was reported by Athwal (1955) who used race 42 from India. This gene was not temperature sensitive. Race 42 was interesting as it also did not attack the varieties Bencubbin, Mentana, Dundee and Uruguay which are susceptible to Australian strains. Athwal concluded from his studies that in each of these varieties a single factor controlled resistance to race 42 and that the factor in Eureka was allelomorphic with the factor in Bencubbin. This gene in Eureka was inherited independently of two factors in Gabo and a single factor in Mentana. The factors for resistance in Mentana and Dundee were independent of each other : Dundee is one of the parents of Eureka. Athwal also considered that the factor for resistance to race 42 in Eureka was allelic or closely linked with the single factor in Uruguay and with one of the two factors in Kenya 117A which confer resistance to race 42.

Gabo, Charter and Yalta

Watson (1941) showed that Kenya 745 (the parent of Charter and Yalta) possessed a single incompletely dominant factor for resistance, and that seedling resistance and field resistance were highly correlated. In the same year Macindoe obtained a similar result with Charter using North American race 34. When crosses between the resistant variety (Gaza $\times$ Bobin^2) and susceptible varieties were studied with race 34, a single major factor controlled resistance in the seedling and adult plant stage. Seedling tests with race 19, however, indicated at least one additional factor for resistance in Charter and (Gaza $\times$ Bobin^2).

On the basis of F_2 data Watson and Waterhouse (1949) classified many wheat varieties into three groups each carrying a major gene present in Kenya 743, Kenya 744 or Kenya 745 respectively. Into the latter group they also placed Gabo, Charter and Yalta.

In 1948, however, Sears and Rodenhiser suggested that two linked, dominant complementary factors were responsible for resistance in crosses between the resistant Timstein and Chinese Spring monosomic lines. Monosomic analysis located these factors on chromosome X, and they were designated Sr11 and Sr12 (Knott, 1959). Similar conclusions were reached by other workers who used the varieties Gabo and Lee in crosses with monosomic lines of Chinese Spring. Lee originated from a Hope $\times$ Timstein cross, and Watson and Stewart (1956) have shown that the varieties Timstein C.I. 12347 and Lee carry the same resistances as Gabo. They concluded that Timstein probably was introduced into the U.S. as a sisterline of Gabo. More recently, a line from a cross Steinwedel $\times$ *T. timopheevi* and carrying the resistance of the latter has been named Timvera (Watson and Luig, 1958).

* Refers to the University of Sydney Wheat Accession Register.

Work by Luig (1960) demonstrated that the Gabo-type resistance was due to a single factor and that this factor was differentially transmitted whenever Mentana was used as the susceptible parent. Sears and Loegering (1961) found evidence for a pollen-killing gene in Chinese Spring located on chromosome X.

Watson (1943) found a second factor in Kenya 745 which operated against four out of 22 standard races against which the single incompletely dominant factor reported earlier (Watson, 1941) gave protection. Both factors seemed to be independent of each other. As mentioned above Athwal (1953) explained the segregation in a cross between susceptible Federation and Gabo to Indian race 42 on the basis of two dominant independent factors, and both these factors were found to be inherited independently of single factors for resistance to this race in Mentana, Bencubbin and Eureka.

Kenya 117*A*

In 1953 Athwal reported a single incompletely dominant factor for resistance in Kenya 117A to four strains of stem rust, while two factors were operative in this variety against Indian race 42. Subsequently Athwal and Watson (1954) found that the single incompletely dominant factor in Kenya 117A was allelic to the factor Sr_{Kb1} in Kenya 744. Seedling and field resistance were correlated, but appeared also to be influenced by modifying factors.

More recently Knott and Anderson (1956) reported that Kenya 117A C.I. 13140 carries three independent genes Sr7, Sr9 and Sr10 for resistance to races 56 and 15B. From tests of isogenic lines of Marquis carrying Sr7, Sr9 and Sr10 with 29 North American and eight Australian strains Green *et al.* (1960) concluded that Sr9b is the same as Sr_{Kb1}, this gene being operative against all eight Australian strains. The lines having Sr7 and Sr10 were only moderately resistant or were susceptible to the eight strains.

Aslam and Ausemus (1958) explained the inheritance of seedling resistance to race 15B in a cross of Mida with Kenya 117A C.I. 12568 on the basis of two or three genes for resistance in Kenya 117A and two genes for susceptibility in Mida. That their results did not agree with the previous findings was probably due to a different strain of Kenya 117A being used. Watson and Stewart (1956) stated that Kenya 117A C.I. 12568 and Australian Kenya 117A W 1347 were dissimilar in their reaction to many strains of stem rust, with the former being the more susceptible. Kenya 117A W 1347, however, was indistinguishable from Kenya 117A C.I. 13140. Omar (1959) reported that the seedling resistance of Kenya 117A to 15B was inherited independently of field resistance to many races of rust.

Sears, Loegering and Rodenhiser (1957) located Sr9 on chromosome XIII, and Knott (1959) found that Sr7 was on chromosome VIII.

Mentana

Although Mentana has been used as an extra-differential variety in several countries, the earlier mentioned work of Athwal (1953) with Indian race 42 is the only report on the inheritance of resistance that has been found during the course of this search of the literature.

Materials and Methods

A short description of the six main varieties used in the present study follows.

Eureka II W 1325. A selection from a cross (Kenya C 6040 × Florence F_1) × Dundee. (Macindoe, 1948).

Gabo W 1422. Bred at Sydney University from a cross (Bobin 39 × Gaza (*T. durum*)) × Bobin 39. (Athwal, 1953).

Charter W 1371. Bred by Dr. S. L. Macindoe from a cross Kenya C 6040 × Gular. In 1948, however, Macindoe stated that the cross was probably made with Kenya C 6042 and not with Kenya C 6040, as Watson had found no segregation for resistance in crosses between Charter and Kenya C 6042 (Macindoe, 1948).

Yalta W 1373. Originated from a cross (Kenya C 6042 × Pusa 4) × Dundee made by Dr. S. L. Macindoe. The spike is square and has short awns, the glumes are pubescent and white, the grain is white.

Mentana W 1124. Athwal and Watson (1957) stated that Mentana W 1124 was different from Mentana Genetic Stock No. 1028. Professor Ugo de Cillis, Italy, has identified Mentana W 1124 as " Ciro Menotti ", also known as Rachael or Awnless Mentana. Ciro Menotti resulted from a cross Akagomuki × (Rieti × Wilhelmina Tarwe) made in 1917. The spike is short awned, semi-compact, somewhat clubby at the tip ; the glumes are glabrous and brown, the grain is white.

Kenya 117A W 1347. Accessioned under C.I. 13140 in the U.S.A. The spike is tip-awned, mid-dense, the glumes are glabrous and white and the grain is red.

The following varieties were used in particular crosses as susceptible parents :

Federation W 107. Bred by W. Farrer from a cross between a selection of Improved Fife and Yandilla.

Little Club W 1. One of Stakman's 12 differential hosts. Very susceptible in the seedling and adult plant stage to all Australian strains of stem and leaf rust of wheat, but semi-resistant to hybrid strains from crosses between *P. graminis* var. *tritici* and *P. graminis* var. *secalis.*

Morocco W 1103. Pedigree unknown. This awned pubescent variety was chosen for this study because of its high susceptibility to all Australian field strains of stem and leaf rust.

Chinese Spring W 1806. Obtained from Dr. E. R. Sears. Susceptible in the seedling stage to all Australian field strains of stem and leaf rust, but resistant to all leaf rust strains as adult plants.

Bobin W 39. The pedigree is unknown as Bobin W 39 is distinct from the commercial Bobin which resulted from a cross between Thew and Steinwedel.

Gular W 1101. Originated from a cross between Wagga 13 and a selection from Marshalls No. 3. Gular is one of the parents of Charter.

Insignia W 1989. Originated from a cross Ghurka × Ranee. It does not carry the gene Sr11 which has been incorporated into its derivatives Insignia 48 and Insignia 49.

Kenya C 6042 W 745. An unnamed crossbred introduced from Kenya Colony.

*II*56.48.1.2.1 W 2691. Developed from an F_2 plant from cross (Little Club × (Gabo^3 × Charter)). More susceptible than Little Club to strains of *P. graminis* var. *secalis.*

Mona W 1168. Cross between Plowman's No. 3 (Bunyip selection) and Canberra.

The material under study comprised the following crosses :

(*a*) Reciprocal crosses in all 30 possible combinations between the six abovementioned varieties.
(*b*) Backcrosses involving the abovementioned crosses.
(*c*) Reciprocal crosses between the six varieties and the susceptible Federation.
(*d*) Crosses involving resistant F_3 lines for the purpose of obtaining lines with single genes for resistance.
(*e*) Crosses between certain varieties to solve special problems which had arisen during the course of these studies.

Inoculations were made and reaction types recorded as described by Stakman and Levine (1922). Rust studies in the field were conducted at Castle Hill Research Station under an artificial epiphytotic.

Designation and description of strains used

In a recent paper Watson and Luig (1963) have proposed a new system of nomenclature for strains of stem rust occurring in the geographical region of Australia and New Zealand. Basically the scheme is the same as Watson and Luig (1961) proposed for leaf rust. According to the new system the numbers preceding the regional designation " Anz " refer to the international set of differential varieties, and the numbers following " Anz " to the six extra-differential varieties, which are numbered in a standardized way: McMurachy (Sr6) — 1, Yalta (Sr11) — 2, W 2402 (Sr9b) — 3, C.I. 12632 (W 1656) — 4, Renown W 2346 — 5, Mentana W 1124 (Sr8) — 6. For example, if an isolate which on the international set conforms to 21 attacks McMurachy and Yalta, but is avirulent on the other four supplementals the designation is strain 21–Anz–1, 2.

Twelve strains of stem rust were used to test the material under study. They represent stock cultures and were frequently checked for contamination. A short description of the strains and their origin is given below:

21–*Anz*–0. Accession Number 57043. A field strain, mainly occurring in Tasmania, New Zealand, and in the southern part of the Eastern Australian Wheat Belt. First identified in 1954 (Watson, 1955), its origin is unknown.

21–*Anz*–2. Accession Number 57072. Several years ago the most prevalent strain in Australia. Was first detected in 1956 and could have arisen as a mutation from 21–Anz–0, or as the result of somatic recombination between 21–Anz–0 and a strain capable of attacking the Yalta type of resistance.

21–*Anz*–2, 6. Accession Number 59137. Not widespread. Origin unknown.

126–*Anz*–6. Accession Number 56196. This is probably identical with the rust first isolated by Waterhouse in 1926 and determined as race 34. It has now been replaced by more virulent strains in the field. Origin unknown. A yellow colour mutant found in the stock culture of 126–Anz–6 was also used. It proved to be identical with the stock culture in its reaction types on differential varieties.

126–*Anz*–1, 6. Accession Number 7316. First identified from Eureka at Narrabri in 1942. This strain is now nearly extinct, but was widespread in the years following 1942 when it first heavily damaged crops of Eureka. Could have originated as a mutation from 126–Anz–6. (Watson and Singh, 1952).

126–*Anz*–2, 6. Accession Number 55350. First reported by Watson, 1955. Its spread in the field has been limited. It is closely related to 126–Anz–6 and 222–Anz–2, 6 and could have arisen as a mutation or as a somatic hybrid.

222–*Anz*–1, 2, 4, 6. Found at Hawkesbury Agricultural College, N.S.W., on genetic material carrying Sr6 and *Triticum timopheevi* resistance, and possibly resulted from a mutation of strain 222–Anz–1, 2, 6. It is distinctly lighter in colour than the other Australian field strains and has also a prolonged incubation period.

NR–7. Obtained as a somatic hybrid between Yellow NR–2 and Red 111–E–2 (Watson and Luig, 1958b).

103–*H*–2*. Obtained as a somatic hybrid between Yellow NR–2 and Red *P. graminis* var. *secalis* (57241) in 1958 (Watson and Luig, 1959). Previous designation M9–a.

* The letter H refers to a laboratory strain of hybrid origin, while E indicates a strain of foreign origin.

111–*E*–2. Obtained from Minnesota, U.S.A. A very avirulent strain of *P. graminis* var. *tritici*, which could have arisen from an intervarietal cross between *P. graminis* var. *tritici* and *P. graminis* var. *secalis*. Described by Watson (1957).

A. 20. Obtained from selfing a culture of *P. graminis* var. *secalis* (57241) (Watson and Luig, 1962). This strain is virulent on Black Winter Rye, but gives also a high reaction on the wheat varieties Yalta and Eureka at temperatures above 75°F.

The rust reaction of eight varieties used in this study to 11 strains of *P. graminis* is given in Table 1.

TABLE 1

Reaction of the six varieties under study and of Federation and Little Club to the eleven selected strains of P. graminis*

Variety	21–0	21–2	21–2, 6	126–6	126–1, 6	126–2, 6	222–1, 2. 4, 6	NR–7	103–H–2	111–E–2	A20
Eureka at 60–65°F	;	;	;	;	3+	;	3	;	;	;	;
Eureka at 75–80°F	3+	3+	3+	3	3+	3	3+	3^{c}	;1+	;1+	3^{cn}
Gabo	;1=	3^{c}	3^{c}	;1=	;1=	3^{c}	3^{c}	3^{c}	;1=	;1=	;
Charter	;1=	3+	3+	;1=	;1=	3+	3	3	;1=	;1=	;
Yalta	;1=	3+	3+	;1=	;1=	3+	3	3+	3^{c}	;1++3^{-c}	3^{c}
Mentana	2	2	3	3+	3+	3+	3	;	;	;	;
Kenya 117A	;2^{-c}	;2^{-c}	;2^{-c}	2^{-n}	2^{-n}	2^{-n}	;1≡	;1, 2^{-n}	;2≡	;2≡	;
Federation	3	3	3+	3+	3+	3+	3+	3	$3^{=c}$	3^{+N}	;1
Little Club	3+	3+	3+	3+	3+	3+	3+	3+	2+	3+	2^{-}

* At temperatures 70°–75°F unless otherwise stated.

EXPERIMENTAL RESULTS

A. Inheritance of resistance to stem rust in the varieties under study

1. *Eureka W* 1325

(*a*) Inheritance of resistance to strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7.

F_1 Studies

At temperatures of 60°–65°F Eureka is resistant to all except two of the strains used in this study. The virulent ones are 126–Anz–1, 6 and 222–Anz–1, 2, 4, 6. As mentioned in the literature review and indicated in Table 1, the resistance of Eureka to most of the former strains is ineffective at high temperatures. F_1 seedlings of crosses between Eureka and the susceptible varieties Little Club, Mentana, Federation and Yalta were tested at temperatures of 60°–65°F. The results are shown in Table 2 and indicate dominance of resistance to strains 126–Anz–6, 126–Anz–2, 6 and NR–7 and incomplete dominance where 21–Anz–2 was used.

F_2 and F_3 Studies

Seedlings of five F_2 families from a cross between Eureka (resistant) and Yalta (susceptible) were tested with strain 21–Anz–2 and seedlings of one of these families were tested with strain NR–7. The tests were carried out at temperatures of 60°–65°F. When analysed statistically the data were homogeneous and indicated a single dominant factor for resistance in Eureka (Table 3).

In 1958, F_2 seedlings from a cross between Gabo (susceptible) and Eureka were tested with strain 126–Anz–2, 6 at day temperatures of 60°–65°F. Out of a total of 204 plants, 48 were susceptible (" 3 + " reaction) and the remainder gave a resistant reaction of a " ; 1 = " type. The F_2 seedlings were tagged according to their reaction type and transplanted into the field at Castle Hill. Later in the year a severe stem rust epiphytotic developed which was mainly caused by 21–Anz–2. All plants which had given a resistant reaction in the seedling stage were resistant or semi-resistant in the field, while the plants

Table 2

Reaction types of F_1 seedlings of crosses between Eureka and susceptible varieties when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7

Susceptible Parent	Strain used	F_1 Reaction
Little Club	126–Anz–6	" ; "
Federation	126–Anz–6	" ; "
Mentana	126–Anz–6	" ; 1 "
Federation	126–Anz–2, 6	" ; "
Yalta	126–Anz–2, 6	" ; "
Federation	NR–7	" ; "
Federation	21–Anz–2	" X "
Yalta	21–Anz–2	" X+ "

which had been susceptible as seedlings reacted similarly in the adult stage. The resulting F_3 generation was tested with strains 126–Anz–2, 6, 21–Anz–2 and NR–7 (Table 4). A similar result was obtained for each F_3 line and from the data it was concluded that a single, dominant factor in Eureka controlled reaction to these three strains.

The results from studies of crosses involving Eureka with Mentana, Little Club, Charter and Federation are given in Tables 3 and 4 and provide further evidence for a single dominant factor hypothesis.

In the foregoing it has been noted that when F_2 plants of the cross (Gabo × Eureka) were studied at Castle Hill in 1958, the one single, dominant factor

Table 3

Segregation of F_2 plants of crosses involving Eureka and susceptible varieties when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7

Susceptible parent	Cross No.	Strain used	Number of seedlings		P-value (3 : 1)
			Resistant	Susceptible	
Yalta	II56.22.1	21–Anz–2	111	41	0·70–0·50
	.2	21–Anz–2	133	55	0·20–0·10
	.3	21–Anz–2	97	27	0·50–0·30
	.4	21–Anz–2	127	55	0·20–0·10
	.5	21–Anz–2	161	60	0·50–0·30
	.1	NR–7	143	47	0·95–0·90
Total			772	285	0·20–0·10
Gabo	II56.9.6	126–Anz–2, 6	156	52	1·00
Mentana	II58.420.1	126–Anz–6	89	32	0·90–0·80
Federation	II58.21.8	126–Anz–6	107	34	0·90–0·80
Charter	II56.24.3	21–Anz–2	146	60	0·20–0·10
Grand Total			1,270	463	0·10–0·05

controlled resistance both in the seedling and adult plant stage. Field studies on F_2 plants of crosses between Eureka and the susceptible varieties Little Club and Federation at Castle Hill in 1960, however, suggested that resistance in Eureka was recessive. In both seasons the field inoculum comprised mainly 21–Anz–2. Of the 147 F_2 plants of cross II58.21.8 (Eureka × Federation), 35 were classified as resistant and 112 as susceptible, while of the 87 F_2 plants of cross II58.84.4 (Little Club × Eureka), 21 were resistant and the remainder susceptible. Classification of adult plants in 1960 was made on the basis of parental reaction: Little Club and Federation were fully susceptible (more than 60% infection) and Eureka was resistant, being less than 15% infected and showing only small pustules.

Table 4

Reaction of F_3 lines of crosses between Eureka and three susceptible varieties when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7

Susceptible parent	Cross No.	Strain used	F_3 Behaviour			P-value (1 : 2 : 1)
			Resist.	Segreg.	Suscept.	
Yalta	II56.22.1	21–Anz–2	39	75	47	0·50–0·30
Gabo	II56.9.6	126–Anz–2, 6 21–Anz–2 NR–7	45	106	48	0·70–0·50
Charter	II56.24.3	21–Anz–2	39	68	40	0·70–0·50
Little Club	II58.84.4	126–Anz–6	19	44	24	0·70–0·50
Total			142	293	159	0·70–0·50

When seedling tests with strain 126–Anz–6 were carried out on the progeny of the F_2 plants from the two crosses it was found that the F_2 plants resistant in the field gave only resistant progeny. Approximately two-thirds of the susceptible F_2 plants gave segregating progeny and one-third gave homozygous susceptible progeny. The combined field and glasshouse data from the cross II56.9.6 (Gabo × Eureka) and from the two above crosses (II58.21.8 and II58.84.4) indicate that plants heterozygous for Sr6 were resistant in the field in 1958 but susceptible in the 1960 season. This was probably due to environmental influences, mainly temperature differences.

(*b*) Inheritance of resistance in Eureka to strain 103–H–2.

The results of seedling tests (Table 1) showed that Eureka was resistant to strains 103–H–2 and 111–E–2 at high temperatures whereas the resistance to certain other strains became ineffective. This suggested that the resistance to 103–H–2 might be due to a gene(s) other than Sr6 and studies were carried out to investigate this possibility.

At day temperatures of above 80°F, 78 F_2 seedlings of the cross Little Club × Eureka were tested with 103–H–2 and the results are presented in Table 5.

Little Club, used as the susceptible parent, gave evidence of some resistance to this strain and this could account in part for the variations obtained in both the intermediate and susceptible classes. Our unpublished work shows that many other varieties in addition to Little Club have genes which operate against strains like 103–H–2 which have arisen from inter-varietal crosses in *P. graminis*. From the broad classification used, however, the data suggest a single factor for high resistance in Eureka.

TABLE 5

Segregation of F_2 plants of the cross (Little Club × Eureka) when tested with strain 103–H–2 at temperatures above 80°F

Parent	Parental reaction	F_2 Segregation			P-value (1 : 2 : 1)
		Resistant (" ; 2 = ")	Intermediate (" 2 —, 2, 3 — c ")	Susceptible (" 2 + +, 3 ")	
Little Club	" 2 + +, 3 + c "	14	42	24	0·30–0·20
Eureka	" ; 2 = "				

Correlated studies on F_3 lines of the cross Gabo × Eureka, using strains 126–Anz–2, 6 and 103–H–2 further indicated that Sr6 was not operative against 103–H–2 at high temperatures. The resistance of Eureka to the latter was due to a second major gene tentatively designated Sr_{E1}.

2. *Gabo W* 1422, *Charter W* 1371 *and Yalta W* 1373

The varieties Gabo, Charter and Yalta will be discussed together as the data from crosses involving these varieties show that they have common factors for resistance to certain strains.

(*a*) Intercrosses between Gabo, Charter and Yalta.

As indicated in the literature review, Gabo, Charter and Yalta were found to possess the same gene (or genes) for resistance to strain 126–Anz–6. To confirm this, F_2 and F_3 generation material of intercrosses between these three varieties was studied (Table 6) and, as expected, no susceptible segregates were found.

TABLE 6

Reaction of F_2 plants and breeding behaviour of F_3 lines of intercrosses involving Gabo, Charter and Yalta when tested with strain 126–Anz–6

Cross	F_2 Segregation			Upper limit of recombination at ·05 level
	Resistant	Susceptible		
Gabo × Yalta ..	788	—		12·65%
Gabo × Charter ..	169	—		26·62%
Charter × Yalta ..	226	—		23·16%
	F_3 Behaviour			
	Resist.	Segreg.	Suscept.	
Gabo × Yalta ..	178	—	—	1·72%
Charter × Gabo ..	93	—	—	3·26%
Charter × Yalta ..	119	—	—	2·54%

(*b*) Crosses between Gabo, Charter and Yalta and susceptible varieties

(i) Inheritance of resistance in Gabo, Charter and Yalta to strains 126–Anz–6 and 126–Anz–1, 6.

F_1 Studies

F_1 seedlings of crosses between the three resistant varieties Gabo, Charter and Yalta and susceptible varieties gave a resistant reaction type (" ; 1 + ") to strain 126–Anz–6, indicating that resistance is completely dominant in the F_1 generation.

F_2 and F_3 Studies

F_2 and F_3 generation material from crosses between the resistant varieties Gabo, Charter and Yalta and the susceptible varieties Eureka and Bobin W 39 were tested with strain 126–Anz–1, 6. Segregation of a single dominant factor pair for resistance in each cross was indicated (Tables 7 and 8). Likewise, F_2 segregation results of crosses between Gabo and Charter and the susceptible Federation, Insignia and Little Club suggested a single dominant factor for resistance.

Data from some F_2 families of crosses (Gabo × Morocco) and (Morocco × Yalta), however, did not fit a single factor hypothesis and in the crosses (II56.48.1.2.1 W 2691 × Gabo) and (Yalta × Federation) and reciprocal, deviations from a three to one ratio were so great that another explanation

Table 7

Results of tests with strain 126–Anz–1, 6 on F_2 populations from crosses between the three resistant varieties Gabo, Charter and Yalta and susceptible varieties

Parents	Cross No. and Family	F_2 Segregation		P-value (3 : 1)
		Resist.	Suscept.	
Gabo × Eureka ..	II56.9.2	335	113	0·95–0·90
Eureka × Gabo ..	II56.20.1	127	48	0·50–0·30
Total		462	161	0·70–0·50
Gabo × Federation ..	II58.42.5	92	32	0·90–0·80
Federation × Gabo ..	II58.32.2	126	47	0·70–0·50
Federation × Gabo ..	.6	310	101	0·90–0·80
Total		528	180	0·80–0·70
Gabo × Morocco ..	II59.345.1	208	73	0·80–0·70
Gabo × Morocco ..	.2	129	59	0·05–0·02
Gabo × Morocco ..	.3	65	15	0·20–0·10
Gabo × Morocco ..	.4	112	44	0·50–0·30
Total		514	191	0·20
Insignia × Gabo ..	II59.358.1	203	82	0·20–0·10
Insignia × Gabo ..	.2	150	50	1·00
Total		353	132	0·30–0·20
II56.48.1.2.1 × Gabo ..	II61.90.5	83	62	<0·001
II56.48.1.2.1 × Gabo ..	.11	111	49	0·20–0·10
Total		194	111	<0·001
Mona × Gabo	II59.383.1	156	50	0·90–0·80
Charter × Eureka ..	II56.40.1	89	31	0·90–0·80
Charter × Federation ..	II58.19.3	279	99	0·70–0·50
Charter × Federation ..	.4	34	12	0·90–0·80
Total		313	111	0·70–0·50
Little Club × Charter	II58.84.3	408	125	0·50–0·30
Yalta × Eureka ..	II58.40.1	59	22	0·70–0·50
Yalta × Eureka ..	.2	96	37	0·50–0·30
Eureka × Yalta ..	II56.22.6	186	61	0·95–0·90
Eureka × Yalta ..	.8	58	19	0·95
Eureka × Yalta ..	II58.419.5	126	44	0·80–0·70
Total		525	183	0·70–0·50

Table 7.—*Continued.*

Results of tests with strain 126-*Anz*-1, 6 *on* F_2 *populations from crosses between the three resistant varieties Gabo, Charter and Yalta and susceptible varieties*—Continued

Parents	Cross No. and Family	F_2 Segregation		P-value (3 : 1)
		Resist.	Suscept.	
Yalta × Federation ..	II58.41.2	54	9	0·05–0·02
Yalta × Federation ..	.3	115	43	0·70–0·50
Yalta × Federation ..	.4	64	20	0·80
Federation × Yalta ..	II58.33.1	26	12	0·50–0·30
Federation × Yalta ..	.2	36	3	0·02–0·01
Federation × Yalta ..	.3	54	18	1·00
Federation × Yalta ..	.5	63	10	0·05–0·02
Federation × Yalta ..	.6	42	22	0·10–0·05
Federation × Yalta ..	.7	21	6	0·80–0·70
Federation × Yalta ..	.8	47	9	0·20–0·10
Federation × Yalta ..	.9	56	26	0·20–0·10
Federation × Yalta ..	.10	118	39	0·98–0·95
Federation × Yalta ..	.11	102	18	0·02–0·01
Federation × Yalta ..	.12	71	21	0·70–0·50
Federation × Yalta ..	.13	244	62	0·10–0·05
Federation × Yalta ..	.14	87	26	0·70–0·50
Total		1,200	344	0·02–0·01
Heterogeneity (3·49 : 1) : $\chi^2 = 30\cdot674$; d.f = 15 ; P-value = 0·01–0·001				
Morocco × Yalta ..	II59.355.2	115	36	0·80–0·70
Morocco × Yalta ..	.3	159	64	0·30–0·20
Morocco × Yalta ..	.4	236	71	0·50–0·30
Morocco × Yalta ..	.5	229	56	0·05–0·02
Morocco × Yalta ..	.6	96	38	0·50–0·30
Morocco × Yalta ..	.7	103	22	0·10–0·05
Total		938	287	0·30–0·20

had to be found. Moreover, the test for heterogeneity of the latter reciprocal cross gave a significant χ^2 value.

When Chinese Spring and Mentana were used as the susceptible parents in crosses with three resistant varieties, the F_2 ratios again did not fit a single factor hypothesis (Tables 9 and 10). While the F_2 data of crosses involving Gabo and Charter proved to be homogeneous when analysed statistically this

Table 8

Reaction of F_3 *lines of three crosses when tested with strain* 126–*Anz*–1, 6

Cross	F_3 Segregation				P-value (1 : 2 : 1)
	Resist.	Segreg.	Suscept.	Total	
Eureka × Yalta ..	37	79	45	161	0·70–0·50
Gabo × Eureka ..	49	103	47	199	0·90–0·80
Charter × Bobin 39	16	34	16	66	0·98–0·95
Total	102	216	108	426	0·90–0·80

was not so of reciprocal crosses of Yalta with Mentana and the χ^2 value from the cross involving Yalta with Chinese Spring also suggested heterogeneity. The F_2 ratios varied according to the F_1 plant from which they came, and apparently no maternal influences were present in the reciprocal crosses.

It has been suggested that this departure from Mendelian segregation in crosses involving Gabo, Charter and Yalta is due to differential transmission of gametes containing the alleles for rust reaction (Luig, 1960; 1964). The data which provided the first conclusive evidence to this were obtained mainly from correlated F_3 studies of stem rust and leaf rust resistance. Mentana is resistant to strain 68–Anz–1, 2, 3 of leaf rust, *Puccinia recondita* Rob. ex Desm., and this resistance was found to be closely linked with the stem rust resistance of Gabo, Charter and Yalta. By testing F_3 lines with the two pathogens (Table 11) it was possible to establish the following: (i) a very close linkage in the repulsion phase between leaf rust and stem rust reaction, so that among

TABLE 9

Segregation of plants of F_2 populations from crosses between the three resistant varieties Gabo, Charter and Yalta and the susceptible varieties Chinese Spring and Mentana when tested with strain 126–Anz–6

Parents	Cross No. and Family	F_2 Segregation		Ratio (Res. : Sus.)	P-value (3 : 1)
		Resist.	Suscept.		
Chinese Spring × Gabo	I161.445.1	163	80	2·0 : 1	0·01–0·001
Chinese Spring × Gabo	.2	144	75	1·9 : 1	0·01–0·001
Chinese Spring × Gabo	.3	133	77	1·7 : 1	<0·001
Chinese Spring × Gabo	.4	214	116	1·8 : 1	<0·001
Total		654	348	1·9 : 1	<0·001
Chinese Spring × Yalta	I161.444.1	24	13	1·8 : 1	0·20–0·10
Chinese Spring × Yalta	.2	11	18	0·6 : 1	<0·001
Chinese Spring × Yalta	.4	26	20	1·3 : 1	0·01–0·001
Chinese Spring × Yalta	.5	47	53	0·9 : 1	<0·001
Chinese Spring × Yalta	.6	21	12	1·9 : 1	0·20–0·10
Chinese Spring × Yalta	.7	12	10	1·2 : 1	0·05–0·02
Chinese Spring × Yalta	.8	48	25	1·9 : 1	0·10–0·05
Total		189	151	1·3 : 1	<0·001
Heterogeneity: $\chi^2 = 11 \cdot 885$; d.fr. = 6; P-value = 0·05–0·02					
Gabo × Mentana ..	I156.7.4	107	51	2·1 : 1	0·05–0·02
Gabo × Mentana ..	.5	83	31	2·7 : 1	0·70–0·50
Mentana × Gabo ..	I156.1.1	85	27	3·1 : 1	0·90–0·80
Mentana × Gabo ..	.2	129	60	2·2 : 1	0·05–0·02
Mentana × Gabo ..	I161.436.1	218	90	2·4 : 1	0·10–0·05
Mentana × Gabo ..	.2	194	95	2·0 : 1	0·01–0·001
Mentana × Gabo ..	.3	118	66	1·8 : 1	<0·001
Total		934	420	2·2 : 1	<0·001
Charter × Mentana ..	I156.37.1	171	80	2·1 : 1	0·02–0·01
Charter × Mentana ..	.2	260	111	2·3 : 1	0·05–0·02
Charter × Mentana ..	.7	69	35	2·0 : 1	0·05–0·02
Total		500	226	2·2 : 1	<0·001

786 F_3 lines none was homozygous resistant to both rusts; (ii) a difference in the segregation ratios according to whether Gabo, Charter or Yalta was used as the parent in crosses with Mentana.

The significance of these results in relation to differential transmission of gametes has already been reported (Luig, 1964).

(ii) Inheritance of resistance in Gabo to strain 21–Anz–2.

The gene Sr11 carried by Gabo, Charter and Yalta is not operative against 21–Anz–2. Gabo gives a "3–c, 3c" type of reaction when tested with this strain while Charter and Yalta are fully susceptible.

When F_2 and F_3 generation material of the cross (Gabo × Charter) was tested with 21–Anz–2, the results suggested that the difference in the reaction

TABLE 10

Reaction of F_2 families of cross Yalta × Mentana and reciprocal to strain 126–*Anz*–6

Family	F_2 Segregation Resist.	F_2 Segregation Suscept.	Ratio	χ^2 (3 : 1)	P-value (3 : 1)	χ^2 (1·29 : 1)	P-value (1·29 : 1)
Yalta × Mentana II56.25							
·1	10	8	1·3 : 1	2·722	·10–·05	0·004	·95–·90
·3	25	11	2·3 : 1	0·593	·50–·30	2·516	·20–·10
·4	34	16	2·1 : 1	1·307	·30–·20	2·767	·10–·05
·5	81	43	1·9 : 1	6·194	·02–·01	4·075	·05–·02
·7	122	129	0·9 : 1	93·260	<·001	6·091	·02–·01
·8	142	109	1·3 : 1	45·452	<·001	0·006	·95–·90
·9	119	122	1·0 : 1	84·383	<·001	4·738	·05–·02
·10	129	82	1·6 : 1	21·626	<·001	1·981	·20–·10
Total	662	520	1·27 : 1			22·178*	·01–·001
Mentana × Yalta II56.4							
·1	79	98	0·8 : 1	87·053	<·001	9·858	·01–·001
·2	119	48	2·5 : 1	1·248	·30–·20	15·103	<·001
·3	160	158	1·0 : 1	103·350	<·001	4·679	·05–·02
·4	109	87	1·3 : 1	39·293	<·001	0·041	·90–·80
·5	99	47	1·1 : 1	4·027	·05–·02	7·829	·01–·001
·6	134	132	1·0 : 1	86·020	<·001	3·836	·10–·05
·7	81	47	1·7 : 1	9·375	·01–·001	2·513	·20–·10
·8	92	53	1·7 : 1	10·320	·01–·001	2·985	·10–·05
Total	873	670	1·3 : 1			46·844*	<·001
Grand Total	1,535	1,190	1·29 : 1			69·022*	<·001

* Heterogeneity χ^2 (1·29 : 1) = 69·022 ; P-value (15 d.f.) = <·001.

TABLE 11

Reaction of F_3 lines of the crosses (*Gabo × Mentana*), (*Mentana × Charter*), (*Mentana × Yalta*) *and* (*Yalta × Mentana*) *to strains* 126–*Anz*–6 *of stem rust and* 68–*Anz*–1, 2, 3 *of leaf rust*

		Reaction to stem rust Resistant	Segregating	Susceptible
Gabo × Mentana				
Reaction to leaf rust	Resistant	—	—	62
	Segregating	—	121	3
	Susceptible	40	—	—
Mentana × Charter				
Reaction to leaf rust	Resistant	—	—	52
	Segregating	—	88	—
	Susceptible	37	1	—
Mentana × Yalta				
Reaction to leaf rust	Resistant	—	—	62
	Segregating	—	84	2
	Susceptible	24	1	1
Yalta × Mentana				
Reaction to leaf rust	Resistant	—	—	107
	Segregating	1	93	2
	Susceptible	4	1	—

types of these two varieties was due to a single factor pair possessed by Gabo (Table 12). Provisionally, this factor is designated Sr_{G1}.

(iii) Inheritance of resistance in Gabo and Charter to strains 103–H–2, 111–E–2 and A20.

As shown in Table 1, Gabo and Charter are highly resistant in the seedling stage to 103–H–2, while Yalta gives a semi-susceptible reaction. Apparently the gene Sr11 does not operate against this strain. To investigate the nature of the resistance to 103–H–2, F_2 and F_3 generation material from crosses between the three varieties was studied. F_1 seedlings of crosses of W2691 ("3" reaction type) × Gabo and Little Club ("2 + +" reaction type) × Charter were resistant ("; 1" reaction type) thus indicating dominance of resistance.

TABLE 12

Reaction of F_2 plants and breeding behaviour of F_3 lines to strain 21–Anz–2 of cross (Gabo × Charter)

F_2 Segregation				P-value
Resistant ("3 — c, 3c")	Intermediate ("3c, 3 + c")	Susceptible ("3 +")	Total	(1 : 2 : 1)
29	62	21	112	0·30–0·20
F_3 Behaviour				
Resistant	Segregating	Susceptible	Total	
5	13	3	21	0·50–0·30

F_2 and F_3 Studies

From a cross (Gabo × Charter), 169 F_2 seedlings were tested with 103–H–2 but no susceptible segregates were found. Likewise, only highly resistant plants were found when 97 F_3 families of this cross were tested. The presence of the same factor pair for resistance to strain 103–H–2 in both varieties is thus suggested. If it is assumed that the genes in Gabo and Charter are non-allelic and dominant, an upper limit of recombination of 3·06% at the 0·95 level of probability could be calculated according to the formula $0 \cdot 05 = \left(1 - p - \frac{p^2}{4}\right)^n$ where p is the recombination value and n the number of F_3 lines tested.

When F_2 populations from a cross Gabo × Yalta were tested with 103–H–2 a single factor difference was obtained. 104 F_2 seedlings gave a reaction as high as that of Yalta or were fully susceptible, while the remaining 306 plants resembled the resistant parent (Table 13).

TABLE 13

Reaction to strain 103–H–2 of F_2 seedlings of the crosses (Gabo × Yalta) and (Charter × Yalta)

Parents or Cross	Parental reaction	F_2 Segregation: Resistant "; 1 ="	Resistant "1 +"	Susceptible "X +, 3c"	Susceptible "3"	Probability (3 Res. : 1 Sus.)
Gabo ..	"; 1 ="					
Yalta ..	"3c"					
II56.10 ..		287	19	80	24	·90–·80
Charter ..	"; 1 ="					
Yalta ..	"3c"					
II56.41.7 ..		124	18	30	9	·30–·20

F_2 plants were tagged according to their reaction type and grown to maturity. Subsequently their breeding behaviour to 103–H–2 was studied (Table 14).

The correlated results indicated that a single major factor pair was responsible for the resistance in Gabo. Variations in reaction type in the resistant and susceptible group are probably due to the action of a minor gene (or genes) in Yalta and/or Gabo.

Further evidence for a single dominant factor for resistance to strain 103–H–2 was obtained from F_2 studies of cross Charter × Yalta (Table 13). Studies using monosomic lines of Chinese Spring indicate that this single factor in Gabo and Charter is located on chromosome XVII (Baker and Luig, unpublished ; McIntosh, unpublished).

TABLE 14

F_3 Breeding behaviour of F_2 plants from cross II56.10.3 (*Gabo* × *Yalta*) *representing different reaction types, when tested with strain* 103–*H*–2

		F3 Behaviour			
		Resistant	Segregating	Susceptible	Total
Reaction types in F_2	" ; 1 — "	43	92	—	135
	" 1 + + "	—	2	6	8
	" X +, 3c "	—	1	38	39
	" 3 "	—	—	8	8
	Total	43	95	52	190

χ^2 for a 1 : 2 : 1 ratio = 0·852 P-value = 0·70–0·50

Studies were also carried out with 111–E–2 and A20 on F_3 generation material of the crosses (Charter × Gabo) and (Gabo × Yalta). Charter and Gabo are fully resistant to these strains, while Yalta at temperatures above 75°F gives a " 3–n " reaction with 111–E–2 and a " 3 " reaction with A20. No susceptible segregates were obtained from 97 F_3 lines of the cross (Charter × Gabo) when tested with the two strains, and this suggested that Charter and Gabo have genes for resistance in common, as was found when testing the same lines with 103–H–2. When 42 F_3 lines of the cross II56.10.3 (Gabo × Yalta) previously tested with 103–H–2 were inoculated with 111–E–2 and with A20 it was evident that the same dominant factor in Gabo was operative against 103–H–2 and against 111–E–2, and that the high resistance to A20 was due to a different single factor. Tentatively these two factors have been designated Sr_{G3} and Sr_{G2}, respectively.

3. *Kenya* 117*A W* 1347

F_1 Studies

The F_1 seedlings from crosses between Kenya 117A and susceptible Federation and reciprocal were inoculated with six strains of stem rust and the results are shown in Table 15. The reaction types varied from a " 3 = c " to a " 3 + c " according to the strain used and indicated incomplete dominance of resistance.

F_2 Studies

When F_2 populations of crosses between Kenya 117A and susceptible varieties were tested with strains 126–Anz–6, 126–Anz–2, 6, 21–Anz–2, 222–Anz–1, 2, 4, 6 and NR–7, varying segregation patterns were obtained. It was evident that the resistance of Kenya 117A was conditioned by more than one factor. As tests were not all carried out under similar environmental conditions it was not possible to make accurate comparisons between segregation ratios obtained with different strains, but there seemed to be fewer susceptible segregates when testing with strains 21–Anz–2 and NR–7.

F_3 Studies

(i) Inheritance of resistance in Kenya 117A in a cross with susceptible Yalta.

Of cross II56.35.2 (Kenya 117A × Yalta) 202 seedlings were transplanted into the field and seed was harvested from 181 plants. When the resulting 181 F_3 families were tested with strain 21–Anz–2, 176 were either resistant or segregated with resistant and susceptible plants and five were susceptible. A ratio of 63 : 1 is proposed (P-value = 0·20–0·10) on the basis of segregation of three independent factor pairs. The detailed results of testing these lines, together with the proposed genotypes, are outlined in Table 16. In two of the eight classes the numbers obtained did not conform to the expected ratio.

Table 15

Reaction of F_1 seedlings of crosses between Kenya 117A and the susceptible varieties Yalta and Federation when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6, 222–Anz–1, 2, 4, 6 and NR–7

Parents or Cross	Strain used	Reaction of parents and of F_1 plants				
		21–2	126–6	126–2, 6	222–1, 2, 4, 6	NR–7
Kenya 117A	.. .. ..	2 =	2 = n	2 = n	2 ≡	2 −
Federation	.. .. ..	3 +	3 +	3 +	3	3 +
Yalta	.. ..	3 +	—	—	—	—
Kenya 117A × Federation		3 =	3 c	—	3 = c	—
Federation × Kenya 117A		3 — c	—	3 c	—	3 c
Yalta × Kenya 117A	..	3 — c	—	—	—	—

There were approximately 20 lines in excess in one class (" Segregating Resistant and Susceptible ") and about the same number was lacking in the other class (" Segregating Resistant, Intermediate and Moderately Susceptible "). This is probably due to plants homozygous for the third factor being classified as susceptible.

The inheritance of resistance of Kenya 117A was also studied by testing the same F_3 families of cross II56.35.2 with strain 126–Anz–2, 6 (Table 16). Results were in most cases similar to those observed when testing with 21–Anz–2. This similarity in behaviour is thought to be due mainly to the segregation of Sr9b, a gene which confers resistance to both strains. The other two factors postulated to be effective against 21–Anz–2, seemed to confer a moderate resistance to 126–Anz–2, 6. One of these factors, presumably Sr10 (Green *et al.*, 1960), gave a " 3 — c, 3c " reaction type when homozygous, while the other factor, presumably Sr7 (Green *et al.*, 1960), produced a " 3 + c " reaction type. It is probable that in some instances the moderate susceptibility of lines carrying Sr7 only was mistaken for full susceptibility, and this would explain the discrepancy of observed and expected numbers in some segregation classes. Additive effects of Sr7 and Sr10 in combination with each other and with Sr9b were also in evidence.

Kenya 117A has noticeably more resistance to 222–Anz–1, 2, 4, 6 than to strains 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–2, 6 and NR–7. But comparatively more susceptible or semi-susceptible F_2 plants and F_3 lines were found when crosses of Kenya 117A with two susceptible varieties were tested with 222–Anz–1, 2, 4, 6. Tests on 128 F_3 families from a cross of Kenya 117A with Yalta (" 3 " reaction type) showed that Kenya 117A carries one gene conferring a high degree of resistance, and a second minor gene conditioning a moderately susceptible reaction (" 3c ") to 222–Anz–1, 2, 4, 6 (Table 16).

Correlated F_3 data indicated that the major gene was the same (Sr9b) as that which gave protection against 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–2, 6 and NR–7, but it was evident that against 222–Anz–1, 2, 4, 6 the gene conferred a much higher degree of resistance. Sr9b conditioned a type " ; 2 = " reaction to 222–Anz–1, 2, 4, 6 when homozygous and a type " 2 — " reaction when heterozygous. With the other five strains Sr9b was incompletely dominant.

The minor gene in Kenya 117A for resistance to 222–Anz–1, 2, 4, 6 is probably Sr10. This gene was also operative against 126–Anz–2, 6 and gave a semi-resistant " 3 — cn " reaction to 21–Anz–2. The third gene reported in Kenya 117A, Sr7, apparently does not condition a reaction on its own to 222–Anz–1, 2, 4, 6 which could be easily distinguished from the reaction type of Yalta ; it might, however, act as a modifier in combination with Sr9b or Sr10.

Finally, F_3 families of the cross I156.35.2 of which sufficient seed was at hand were tested with NR–7. This strain originated as a somatic hybrid from two North American strains and one of the objectives for using it was to confirm the previous assumption (Green *et al.*, 1960) that the three factors which condition reaction types in segregating material of cross (Kenya 117A × Yalta) are identical with the three genes Sr7, Sr9b and Sr10. Only 68 F_3 families were tested with NR–7, but it was evident from the results that the three factors which conditioned reaction to the other three strains were also operative against NR–7.

In an attempt to isolate F_3 lines which carry only one of the three factors for resistance in Kenya 117A, seedling tests with the above-mentioned four strains were simultaneously carried out on selected lines of cross I156.35.2 at temperatures ranging from 60° to 70°F. Three lines were found which were homozygous for each of the three genes, and one line which apparently carried both Sr7 and Sr10. The reaction types produced by these lines together with those of their parents, Yalta and Kenya 117A, are shown below :

Proposed genotype	Line or variety	Strain used				
		21–2	126–2, 6	222–1, 2, 4, 6	NR–7	21–2, 3*
Sr7	246	3 c	3 + c	3 + c	3 + c	
Sr9b	256	2 —	2 — c	; 2 =	2 +	3 +
Sr10	244	3 — cn	3 — c	3 c	3 — c	
Sr7, Sr10	2,121	3 = cn	3 = c	3 — c	3 = c	
—	Yalta	3 +	3 +	3 + c	3 +	3 +
Sr7, Sr9b, Sr10	Kenya 117A	2 — n	2 = n	; 2 =	2 —	3 = c

* This strain was obtained from the 1960 Cereal Rust Survey. It is virulent on the isogenic Marquis-line W2402 (obtained from Dr. D. R. Knott) and on the variety Festival, both of which carry Sr9b.

(ii) Inheritance of resistance in Kenya 117A in a cross with susceptible Mentana.

The mode of inheritance of resistance in Kenya 117A to the Australian field strain 126–Anz–6, which has been used extensively in inheritance studies by other workers, was also studied. Yalta, used as the susceptible parent in the cross I156.35.2, is resistant to 126–Anz–6 and therefore the resistance of Kenya 117A to 126–Anz–6 could not be studied in this cross. Cross I156.5.3 (Mentana × Kenya 117A) was used instead as Mentana is susceptible to 126–Anz–6 as well as to 126–Anz–2, 6, 21–Anz–2, 6 and 222–Anz–1, 2, 4, 6. Mentana gives only a semi-resistant " 2 " type of reaction to 21–Anz–0 and 21–Anz–2.

When 126 F_3 lines of cross I156.5.3 were inoculated with 126–Anz–6, the results indicated segregation of two independent and incompletely dominant

TABLE 16

*Distribution of F_3 lines of the cross II*56.35.2 (*Yalta* × *Kenya* 117*A*) *for reaction to strains* 21–*Anz*–2, 126–*Anz*–2, 6 *and* 222–*Anz*–1, 2, 4, 6, *and proposed genotypes for the segregation classes*

Strain	F₃ Rust behaviour and proposed genotypes								Total
	R	Seg. R, I & MS	I	Seg. I & MS	MS	Seg. R & S	Seg. I, MS & S	S	
21–Anz–2	44	21	6	7	5	74	19	5	181
(Expected numbers)	(45·3)	(39·6)	(5·7)	(11·3)	(2·8)	(50·9)	(22·6)	(2·8)	
126–Anz–2, 6	34	12	6	2	4	54	15	4	131
(Expected numbers)	(32·8)	(28·7)	(4·1)	(8·2)	(2·0)	(36·8)	(16·4)	(2·0)	
Proposed genotypes and fraction of total	AABBCC AABBCc AABBcc AABbCC AABbCc AABbcc AAbbCC AAbbCc AAbbcc	AaBBCC AaBBCc AaBBcc AaBbCC AabbCC	aaBBCC aaBBcc	aaBBCc aaBbCC	aabbCC	AaBbCc AaBbcc AabbCc Aabbcc	aaBbCc aaBbcc aabbCc	aabbcc	
	16/64	14/64	2/64	4/64	1/64	18/64	8/64	1/64	

Strain	F₃ Rust behaviour and proposed genotypes						Total
	R	Seg. R & MS	MS	Seg. R & S	Seg. MS & S	S	
222–Anz–1, 2, 4, 6	30	12	9	54	15	8	128
(Expected numbers)	(32)	(16)	(8)	(48)	(16)	(8)	
Proposed genotypes and fraction of total	AABB AABb AAbb	AaBB	aaBB	AaBb Aabb	aaBb	aabb	
	4/16	2/16	1/16	6/16	2/16	1/16	

Explanation of abbreviations: R —resistant; I —intermediate; MS—moderately susceptible; S —susceptible; Seg.—segregating.

Proposed genes: A—Sr9b; B—Sr10; C—Sr7.

factor pairs (Table 17). The two factors, however, were not equal in the degree of resistance they conferred on the F_3 plants. The major factor, which is later shown to be Sr9b, imparted a high resistance (type "2 —" reaction) when homozygous, while the minor factor conditioned a reaction type ranging only from "3 — n" to "3c". This variation in reaction type of F_3 lines thought to possess the minor gene in the homozygous state could be due to the action of a modifying factor, and/or environmental influences.

Strains 126–Anz–2, 6 and 21–Anz–2, 6 were also used to inoculate these F_3 families. The inheritance of resistance in Kenya 117A to the former in

TABLE 17

*Distribution of F_3 lines of cross II*56.5.3 (*Mentana* × *Kenya* 117*A*) *for reaction to strain* 126–*Anz*–6, *and proposed genotypes for the segregation classes*

	Behaviour of F₃ lines and their proposed genotypes							Total
	Segreg. "2—n", "2—"	"2—"	Segreg. "2—n", "3—c"	"3—c"	Segreg. "2—n", "3+"	Segreg. "3—c", "3+"	"3+"	
Actual numbers	25	11	15	3	44	20	8	128
Expected numbers	24	8	16	8	48	16	8	128
Proposed genotypes	AABB AABb	AAbb	AaBB	aaBB	AaBb Aabb	aaBb	aabb	

χ^2 for a 3 : 1 : 2 : 1 : 6 : 2 : 1 ratio = 5·688 P-value (6 d.fr.) = 0·50–0·30 cross II56.35.2 has been reported above and Green *et al.* (1960) have shown a close similarity in the reaction types produced by strains 126–Anz–6 and 126–Anz–2, 6 on isogenic Marquis lines carrying genes Sr7, Sr9b or Sr10. As expected, lines tested with 126–Anz–6 and 126–Anz–2, 6 gave the same reactions to each strain, suggesting that the major factor for resistance to 126–Anz–6 was Sr9b, while the minor factor was presumably Sr10. Mentana itself gives a " 3 " type reaction to these two strains and it is possible that F_3 lines carrying only Sr7 were not significantly more resistant than Mentana.

When the reaction types on F_3 lines to strains 126–Anz–6 and 21–Anz–2, 6 were compared two at a time it was evident that several lines carried more resistance to the latter strain than to the former. This was not unexpected, as 21–Anz–2, 6 probably originated from 21–Anz–2 and thus would be similarly constituted in regard to most genes for pathogenicity. When studying cross II56.35.2 it was found that the factor Sr7 conferred a higher resistance to 21–Anz–2 than to 126–Anz–2, 6. Therefore the presence of Sr7 presumably accounted for the higher resistance of some F_3 lines to 21–Anz–2, 6 than to 126–Anz–6.

Field Studies

During the years 1958–1960 segregating material of the two above-mentioned crosses and of other crosses involving Kenya 117A was studied under field conditions at Castle Hill Research Station, strain 21–Anz–2 contributing most of the inoculum. Classification of adult plants was made on the basis of percentage of rust and size of pustules. Plants with less than 30% infection of stem and with pustules small to medium in size were classified as resistant, and plants showing mainly large confluent pustules and/or carrying more than 30% infection were classified as susceptible.

The mature plant reactions of 181 F_2 plants of cross II56.35.2 (Yalta × Kenya 117A) were recorded and the behaviour in the field of the progenies of these plants was studied in the F_3 and F_4 generations. Kenya 117A was resistant in the field, showing only small pustules on stems less than 10% infected, while Yalta was extremely susceptible (summer sowings of Kenya 117A, however, showed a much higher degree of infection). Nine F_2 plants of the cross II56.35.2 susceptible in the seedling stage to 21–Anz–2 were susceptible as adult plants. However, 94 of 172 resistant F_2 seedlings were also susceptible in the adult plant stage and the remainder were resistant.

The results of the F_3 field tests were compared for each line with F_3 seedlings tests with 21–Anz–2 and it was evident that many F_3 lines resistant or segregating to 21–Anz–2 as seedlings were susceptible as adult plants. These findings can be explained by the incomplete dominance of gene Sr9b and by assuming that the other two genes, Sr7 and Sr10, become ineffective in the adult plant. There was, however, evidence which suggested that these latter genes acted as modifiers in combination with Sr9b. The above results would indicate that selection for resistance of Kenya 117A to 21–Anz–2 in the F_2 generation is of only limited value in breeding procedures.

When seedling reactions of F_3 lines to 126–Anz–2, 6 and NR–7 were compared with the behaviour of these lines under field conditions, the same lack of correlation as in the case of 21–Anz–2 was found. This was expected, as many lines reacted similarly to the three strains.

There was, however, good correlation between seedling reaction to 222–Anz–1, 2, 4, 6 of F_3 lines and their behaviour to stem rust in the field. The comparative data are shown in Table 18. In classifying seedling reaction only the major factor for resistance (Sr9b) was considered and it can be seen that all except two of the 32 families classified as susceptible to 222–Anz–1, 2, 4, 6 in the seedling stage were also susceptible in the field to a combination of strains consisting mainly of 21–Anz–2. The two families which were classified as segregating in the field probably comprised susceptible plants and plants which had escaped infection to a large degree. These results indicate that no gene (or genes) of Kenya 117A other than Sr9b can confer field resistance to 21–Anz–2. Of the 30 F_3 lines which in seedling tests appeared to be homozygous for Sr9b, 25 lines were found to be resistant in the field, a further indication that Sr9b is the main factor for field resistance in Kenya 117A. However, 21 out of 66 families, apparently heterozygous for this gene, were classified as susceptible in the field. It is possible that resistant adult plants were present in the 21 lines, but were not classified as such.

TABLE 18

Distribution of F_3 lines of the cross Yalta × Kenya 117A for reaction to a collection of strains in the field, being mainly 21–Anz–2, and for seedling reaction to 222–Anz–1, 2, 4, 6

Seedling reaction to 222–Anz–1, 2, 4, 6		Behaviour in the field		
		Resistant	Segregating	Susceptible
Resistant	30	25	3	2
Segregating	66	4	41	21
Susceptible	32	—	2	30
Total	128	29	46	53

In 1958, F_2 plants of cross II56.5.3 (Mentana × Kenya 117A) were also studied for their reaction in the field. Mentana was moderately susceptible in the field, showing approximately 40 to 60% infection on stems with pustules of medium size. Of the 122 F_2 plants, 21 were found to be resistant and 101 were classified as susceptible. In some cases, however, difficulties were experienced in making the classification. As mentioned before, the progenies of these F_2 plants were tested in the seedling stage with strains 126–Anz–6, 126–Anz–2, 6 and 21–Anz–2, 6, and when the results of the seedling tests were compared for each F_3 line with the mature plant reaction of the corresponding F_2 plant, it was evident that the same, single, major factor for resistance was operating in the seedling and adult plant stage (Table 19). Of the 21 resistant F_2 plants all, except one, carried the gene Sr9b either in the homozygous or heterozygous condition. Thus the findings on the nature of mature plant resistance in Kenya 117A in this cross are in agreement with those for cross II56.35.2

TABLE 19

Reaction in the field of F_2 plants of the cross Mentana × Kenya 117A and seedling reaction of F_3 lines raised from these plants when tested to strains 126–Anz–6, 126–Anz–2, 6 and 21–Anz–2, 6

Behaviour of F_3 lines	Proposed genotype* of F_2 plant	No. of F_3 lines	Field reaction of F_2 plant	
			Resistant	Susceptible
All 2—n, 2—c, 2—	AABB AABb	25	9	16
All 2—	AAbb	11	3	8
Segregating 2—n, 2—, 3—c, 3c	AaBB	15	3	12
Segregating 2—, 3=c, 3+ ..	AaBb Aabb	44	5	39
All 3—c, 3c	aaBB	3	—	3
Segregating 3—c, 3+	aaBb	16	—	16
All 3+	aabb	8	1	7
Total		122	21	101

* A = Sr9b; B = Sr10

In 1960, 91 F_2 plants of cross II58.73.3 (Kenya 117A × Federation) were studied for their behaviour to stem rust in the field. Of these plants 25 were resistant or semi-resistant, the remaining 66 were semi-susceptible or susceptible. A ratio of one resistant to three susceptible is indicated (P-value = 0·70–0·50), and this is further evidence for a single major factor for adult plant resistance in Kenya 117A. The semi-resistant and semi-susceptible plants carried approximately 20 to 30 and 40 to 60% infection, respectively, and this variation could be due to the action of the modifying genes Sr7 and Sr10 in combination with Sr9b in the heterozygous condition.

4. *Mentana W* 1124

(i) Inheritance of the resistance in Mentana to strain 21–Anz–2 of stem rust.

F_1 Studies

When tested with strain 21–Anz–2 Mentana gave a semi-resistant " ; 2, 3 — c " reaction type. F_1 seedlings from crosses of Mentana with susceptible varieties gave a type " 3 — c, 3c " reaction with this strain thus indicating incomplete dominance of resistance.

F_2 and F_3 Studies

The segregation of reaction in F_2 plants to strain 21–Anz–2 in crosses of Mentana with Yalta and Federation are given in Table 20. A single, incompletely dominant factor pair for resistance in Mentana is indicated, as the data fit a ratio of one resistant : two intermediate : one susceptible. The resistant F_2 seedlings gave a type " ; 2, 3 — c " reaction similar to that of Mentana, the intermediate exhibited a " 3c " reaction type, and the susceptible were as susceptible as Yalta or Federation.

TABLE 20

F_2 segregation to strain 21–Anz–2 of crosses involving Mentana and susceptible varieties

Susceptible parent	Cross No. and family	F_2 Segregation			P-value (3 : 1) (R + I : S)	P-value (1 : 2 : 1)
		Resist.	Inter.	Suscept.		
Yalta	II56.4.1	19	41	22	0·70	0·90–0·80
Federation	II58.86.1	65	112	52	0·50–0·30	0·50–0·30
Federation	II58.86.2	68	133	61	0·70–0·50	0·90–0·80
Total		152	286	135	0·50–0·30	0·70–0·50

Two crosses between Mentana and susceptible varieties were studied in the F_3 generation for their reaction to 21–Anz–2 (Table 21). The data fit a 1 : 2 : 1 ratio and thus provide further evidence for monofactorial segregation in crosses between Mentana and susceptible varieties. Recent work has indicated that this factor is the same as Sr8 (Watson and Luig, 1963).

TABLE 21

Segregation of F_3 lines of crosses between Mentana and susceptible Federation and Yalta for reaction to strain 21–Anz–2

Cross	F_3 Segregation				P-value (1 : 2 : 1)
	Resistant	Segregating	Susceptible	Total	
Federation × Mentana	12	12	8	32	0·30–0·20
Yalta × Mentana	14	31	11	56	0·70–0·50
Total	26	43	19	88	0·70–0·50

(ii) Inheritance of resistance in Mentana to strain NR–7.

F_1 Studies

Mentana is fully resistant to this strain and shows a " ; " reaction type. Yalta is susceptible and Federation and Chinese Spring moderately susceptible (" 3 + cn " and " 3 " type reactions respectively). F_1 seedlings of crosses between Mentana and the latter three varieties when tested with NR–7 gave " X, 3 — c " reaction types, thus indicating that resistance was incompletely dominant.

F_2 and F_3 Studies

The F_2 and F_3 data from a cross between Yalta and Mentana are set out in Table 22, and they can be best explained on the basis of two independent, incompletely dominant factors for resistance present in Mentana. A high correlation between F_2 and F_3 reaction was obtained in spite of the incomplete dominance of resistance indicated by F_1 tests. Eight distinct F_3 behaviour patterns were observed and genotypes were assigned to them by assuming that Mentana possesses two factor pairs for resistance. One factor pair conditions an " X = " reaction in the homozygous and an " X + " reaction in the heterozygous state, while the second produces a moderately resistant reaction of a " 2, 3 — c " type in the homozygous and a semi-susceptible " 3c " reaction type in the heterozygous state. The statistical analysis shows close agreement between the observed numbers of plants and those expected on this hypothesis.

TABLE 22

Correlated data showing reaction to strain NR–7 of F_2 plants of the cross Yalta (susceptible) × Mentana (resistant) and of F_3 lines raised from the F_2 plants

Reaction in F_2	Number of F_2 plants	Behaviour and reaction in F_3: " ;1= "	Segreg. " ;1= " and " X = "	" X= "	Segreg. " ;1= ", " X= " & " 3–c "	Segreg. " ;1= " and " 3+ "	" 2, 3–c "	Segreg. " 2 " and " 3+ "	" 3+ "	Number of F_3 lines
" 0 "	3	—	—	—	—	—	—	1	—	1
" ;1= "	9	7	—	1	1	—	—	—	—	9
" ;1 "	22	1	14	2	1	2	1	—	—	21
" X "	51	—	4	2	8	25	3	7	—	49
" 3c "	24	—	—	—	1	12	—	6	4	23
" 3+ "	11	—	—	—	—	5	—	2	2	9
Total	120	8	18	5	11	44	4	16	6	112
Suggested genotype		CCDD	CCDd	CCdd	CcDD	CcDd Ccdd	ccDD	ccDd	ccdd	
Expected number of F^3 lines		7	14	7	14	42	7	14	7	112
		$\chi^2 = 4{\cdot}336$			P-value (7 d.fr.) = 0·80–0·70					

Further evidence for two factor pairs for resistance to NR–7 in Mentana was obtained in a cross with susceptible Charter (Table 23). The F_2 and F_3 segregations of this cross followed very closely those observed in the cross where Yalta was the susceptible parent, and again a non-significant χ^2-value for the eight segregation classes was obtained.

In order to obtain lines which carry only one of the two postulated major genes for resistance to NR–7, two lines from the cross (Yalta × Mentana) were selected : " 1841 " apparently homozygous for a factor pair giving a " 3 — c " reaction, and " 1843 " which appeared to carry a factor pair conditioning a " X = " reaction. A cross was made between these two lines and each line was also crossed with the moderately susceptible Federation.

The F_1 plants of these crosses when tested with NR–7 gave a reaction similar to that of F_1 plants from crosses between Mentana and susceptible varieties. In the following year F_2 populations from these crosses were tested

TABLE 23

Correlated data showing reaction to strain NR–7, of F_2 plants of the cross Charter (susceptible) × Mentana (resistant) and of F_3 lines raised from the F_2 plants

Reaction in F_2	Number of F_2 plants	Behaviour and reaction in F_3: ";1="	Segreg. ";" to "X="	"X="	Segreg. ";" to "3–c"	Segreg. ";" to "3+"	"2", "3–c"	Segreg. "2" to "3+"	"3+"	Number of F_3 lines
";1="	30	12	14	2	2	—	—	—	—	30
"1+"	36	—	7	2	17	7	1	2	—	36
"X"	81	—	2	2	6	45	6	10	—	71
"3c"	6	—	—	—	—	1	—	1	4	6
"3"	7	—	—	—	—	1	—	—	4	5
Total	160	12	23	6	25	54	7	13	8	148
Suggested genotype		CCDD	CCDd	CCdd	CcDD	CcDd Ccdd	ccDD	ccDd	ccdd	
Expected number of F_3 lines		9·25	18·5	9·25	18·5	55·5	9·25	18·5	9·25	148
		χ^2 = 7·731			P-value (7 d.fr.) = 0·50–0·30					

with NR–7 and 21–Anz–2 (Table 24). A single factor segregation was indicated in cross ("1841" × Federation) with both strains. F_2 seedlings of cross ("1843" × Federation) segregated in a ratio of approximately three resistant to one susceptible when tested with NR–7, but were all susceptible to strain 21–Anz–2. F_2 tests with strain NR–7 on cross ("1843" × "1841") gave a similar segregation pattern to that obtained previously in F_2 populations from crosses between Mentana and susceptible varieties. These findings suggest that lines "1841" and "1843" together possess the full resistance of Mentana to NR–7 and that each line carries a single factor pair for resistance to it. "1841" carries the factor pair Sr8 which also gives protection from 21–Anz–2 in the seedling stage, and "1843" possesses the factor pair which confers the higher type of resistance to NR–7 (";1 + 3 — n" reaction) but no resistance to 21–Anz–2. This factor is tentatively designated Sr_{M1}.

TABLE 24

Reactions of F_2 seedlings of crosses involving the two resistant lines "1841" and "1843" when tested with strains 21–Anz–2 and NR–7

Parents	Strain used	F_2 Segregation and reaction: ;	;2^{-n}	;2^{-}	X, 3^{-n}	2^{+cn}	3^{-c}, X+	3^{-c}, 3^{c}	3^{c}, 3^{+c}	3, 3+	Ratio	P-value
1843 × Federation	21–Anz–2	—	—	—	—	—	—	—	—	69	—	—
1843 × Federation	NR–7	—	—	—	16	—	38	—	—	27	1 : 2 : 1	0·20–0·10
1841 × Federation	21–Anz–2	—	—	—	—	—	—	47	69	40	1 : 2 : 1	0·30–0·20
1841 × Federation	NR–7	—	—	—	—	—	—	56	91	54	1 : 2 : 1	0·50–0·30
1843 × 1841	NR–7	6	18	20	9	25	23	13	15	10	15 : 1	0·70–0·50
Proposed genotype of F_2 plant		CCDD	CCDd	CcDD	CCdd	CcDd	Ccdd	ccDD	ccDd	ccdd		

B. The linkage relationship of genes controlling reaction to stem rust

As indicated in the foregoing, several factors for resistance to stem rust were found in the six varieties under study. The possibility of linkage between these factors was considered and the appropriate tests were carried out. Results from F_2 and F_3 generation material of crosses between Eureka and the varieties Gabo, Yalta and Charter are shown in Tables 25 and 26. Eureka carries a single gene for resistance (Sr6) to strain 126–Anz–6 on chromosome XX (2D) and Gabo, Yalta and Charter all carry the gene Sr11 for resistance to strain 126–Anz–6 on chromosome X (6B). In certain instances Sr11 is differentially transmitted, but this was not the case in crosses with Eureka. The statistical analysis showed that the data agreed with the hypothesis of two dominant independent factors (Tables 25 and 26).

TABLE 25

Segregation in F_2 populations of crosses between resistant varieties

Cross	Strain used	F_2 Segregation		Expected ratio	P-value
		Resistant	Susceptible		
Gabo × Eureka	126–Anz–6	135	6	15 : 1	0·50–0·30
Eureka × Yalta.. ..	126–Anz–6	215	14	15 : 1	0·95–0·90
Charter × Eureka ..	126–Anz–6	469	30	15 : 1	0·90–0·80
Kenya 117A × Eureka	21–Anz–2	304	2	255 : 1	0·80–0·70
Gabo × Eureka	103–H–2*	244	13	15 : 1	0·50–0·30

* The testing was conducted at temperatures above 80°F.

No evidence of linkage was found between the gene Sr6 in Eureka and the genes for resistance to 21–Anz–2 in Kenya 117A (Table 25). It has been postulated that three factors operate in Kenya 117A against 21–Anz–2, of which two, Sr7 and Sr9b, have been located by previous workers on chromosomes VIII (4B) and XIII (2A) respectively.

The close linkage of Sr11 with a factor for leaf rust resistance in Mentana was discussed earlier. In Table 26 it is shown that Sr11 in Yalta and the factor for resistance to strain 103–H–2 in Eureka, tentatively designated Sr_{E1}, were inherited independently of each other. No linkage was found between Sr_{E1} and the factor for resistance (Sr_{G2}) to 103–H–2 in Gabo (Table 25).

TABLE 26

Reaction of F_3 lines of the crosses (Eureka × Yalta) and (Gabo × Eureka) when tested with strains 126–*Anz*–1, 6 *and* 126–*Anz*–2, 6 *and of the cross (Eureka × Yalta) when tested with strains* 126–*Anz*–1, 6 *and* 103–*H*–2

Eureka × Yalta		Reaction to 126–Anz–1, 6				χ^2	P-value (4 d.fr.)
		Resist.	Segreg.	Suscept.	Total		
Reaction	Resistant	10	20	9	39		
to	Segregating	19	32	24	75		
126–Anz–2, 6	Susceptible	8	27	12	47		
	Total	37	79	45	161	2·597	0·70–0·50

Gabo × Eureka		Reaction to 126–Anz–1, 6				χ^2	P-value (4 d.fr.)
		Resist.	Segreg.	Suscept.	Total		
Reaction	Resistant	10	25	10	45		
to	Segregating	25	55	26	106		
126–Anz–2, 6	Susceptible	14	23	11	48		
	Total	49	103	47	199	0·903	0·95–0·90

Eureka × Yalta		Reaction to 103–H–2*				χ^2	P-value (4 d.fr.)
		Resist.	Segreg.	Suscept.	Total		
Reaction	Resistant	2	2	1	5		
to	Segregating	5	4	4	13		
126–Anz–1, 6	Susceptible	3	9	3	15		
	Total	10	15	8	33	2·689	0·70–0·50

* The testing was conducted at temperatures above 80°F.

The two independent factors for resistance to NR–7 in Mentana, Sr8 and Sr_{M1}, did not show any linkage with Sr11 in the cross (Yalta × Mentana).

The three genes for stem rust resistance in Kenya 117A appeared also to be inherited independently of the following genes: Sr11 and Sr_{G2} in the crosses (Gabo × Kenya 117A) and (Kenya 117A × Gabo); and Sr8 in the cross (Kenya 117A × Mentana).

A study was also made of the segregation of two morphological characters, brown chaff colour and glume pubescence, in relation to stem rust reaction.

Table 27

Probable genotypes of six varieties of wheat regarding genes for resistance to stem rust

Variety	Genotype										
Eureka	Sr6										Sr_{E1}
Gabo						Sr11	Sr_{G1}	Sr_{G2}	Sr_{G3}		
Charter						Sr11		Sr_{G2}	Sr_{G3}		
Yalta						Sr11					
Kenya 117A		Sr7		Sr9b	Sr10						
Mentana			Sr8							Sr_{M1}	

The single factor for pubescent glume in Yalta was inherited independently of the following genes for stem rust resistance: Sr6, Sr8, Sr9b, Sr11, Sr_{G2} and Sr_{M1}. The factor for pubescent glume has been located on chromosome XIV (1A) (Sears, 1953).

The single factor for brown chaff in Eureka was inherited independently of Sr11 and of Sr6. Unrau (1950) has located a single gene for brown chaff colour on chromosome I (1B).

The following Tables 27 and 28 summarize the results of these studies as to the genetic constitution of the six varieties and as to the nature of the resistance conferred by the different genes.

Table 28

Nature of resistance conferred by eleven genes possessed by six wheat varieties

Gene	Dom. or Rec.*	Possessed by Variety	Controls resistance to strain**
Sr6***	D	Eureka	21–Anz–0, 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, NR–7, 103–H–2, 111–E–2
Sr_{E1}	d	Eureka	103–H–2
Sr11	D	Gabo Charter Yalta	21–Anz–0, 126–Anz–6, 126–Anz–1, 6
Sr_{G1}	r	Gabo	21–Anz–0, 21–Anz–2, 126–Anz–6
Sr_{G2}	D	Gabo Charter	103–H–2 and 111–E–2
Sr_{G3}	D	Gabo Charter	A20
Sr7	d	Kenya 117A	21–Anz–0, 21–Anz–2, 21–Anz–2, 6
Sr9b	d	Kenya 117A	21–Anz–0, 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6, NR–7, 222–Anz–1, 2, 4, 6
Sr10	d	Kenya 117A	21–Anz–0, 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6, NR–7
Sr8	r	Mentana	21–Anz–0, 21–Anz–2, NR–7
Sr_{M1}	r	Mentana	NR–7

* D = dominant; d = incompletely dominant; r = recessive.
** Includes only the eleven strains listed in Table 1.
*** Temperature-sensitive.

Discussion

The results of the studies on the nature of resistance to stem rust in six wheat varieties reported herein show that single independent factors were operating to individual strains. In certain cases the segregation ratios were distorted by a differential transmission rate for the gametes carrying genes located on chromosome X (6B). The segregation ratios were also altered by genes which had a cumulative effect in modifying the dominant or recessive condition and by temperature effects changing the expression of the factors for resistance.

The latter was the case with the gene Sr6 of Eureka, which becomes ineffective at temperatures above 80°F. Hence when Eureka is crossed with susceptible varieties and the progenies are studied at low temperatures (60° to 65°F) an F_2 ratio of three resistant to one susceptible is obtained with strains 21–Anz–2, 126–Anz–6 and NR–7. At higher temperatures of 65° to 70°F the heterozygous class can be distinguished from the resistant class when testing with 21–Anz–2. The intermediate, heterozygous F_2 seedlings still give a necrotic reaction, but the type " ; 1 = " reaction has changed into a type " 1 + +, 3 — n " reaction. A similar segregation pattern is obtained with strains 126–Anz–6 and NR–7 at temperatures of 70° to 75°F. At these temperatures, however, it is no longer possible to decide between intermediate and susceptible seedlings when testing with 21–Anz–2. With this strain the initial ratio of three to one has thus changed into a one to three ratio, with the resistant plants giving the same reaction at 70° to 75°F as the intermediates at temperatures of 65° to 70°F. At temperatures above 75°F, F_2 seedlings are all moderately susceptible or susceptible to 21–Anz–2, and at temperatures above 80°F the gene Sr6 is no longer effective against 126–Anz–6 or NR–7. Hence when testing at temperatures of 70° to 75°F with strains 21–Anz–2, 126–Anz–6 and NR–7 it can be assumed that the gene Sr6 is recessive with 21–Anz–2 and incompletely dominant with the latter two strains. Such has been suggested by Knott and Anderson (1956), who found that Sr6 was dominant with race 56 but recessive with race 15B. The reaction types recorded on Eureka to seven strains listed in Table 1, at various temperatures, suggest that genetic material in which Sr6 segregates would behave similarly to strains 21–Anz–0, 21–Anz–2 and 21–Anz–2, 6. With the other four strains, 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6, and NR–7, the same single factor is operating, but with a somewhat higher degree of resistance.

No differential transmission rate exists for alleles at the Sr6 locus. Eureka possesses no other factors for resistance to Australian field strains. However, when an avirulent laboratory strain, 103–H–2, which had its origin in a somatic cross between *P. graminis* var. *tritici* and *P. graminis* var. *secalis*, was used, segregation of a second, incompletely dominant factor pair was evident. Whether this factor is identical with the second factor for resistance in Eureka, as reported by Athwal (1955), cannot be ascertained. Athwal worked with race 42 from India, and he found that the varieties Bencubbin, Mentana, Dundee, Uruguay and Gabo, which are susceptible to several Australian strains, were resistant to race 42. Strain 103–H–2 is also non-pathogenic on these five varieties. Hence, it is likely that the same factor in Eureka conditions resistance to 103–H–2 and to race 42.

The gene Sr11, possessed by Gabo, Charter and Yalta, has been shown to be differentially transmitted in crosses between each of these three varieties and certain other varieties including Chinese Spring. This finding explains why several investigators using the latter variety as the susceptible parent postulated two, linked, dominant complementary factors for this type of resistance, while other workers who used different susceptible varieties reported a single factor pair. Further results on, and several aspects of, differential transmission have been discussed elsewhere (Luig, 1961 ; 1964).

While it has been known for many years that Gabo, Charter and Yalta carry the same resistance (Sr11) to particular Australian field strains (Watson and Waterhouse, 1949), it was also noticed that when these strains were present in the field Gabo was not as severely attacked as Charter, and Charter was less affected than Yalta (Waterhouse, 1952). It was thought that the early maturity of Gabo enabled this variety to escape infection to a certain extent and, while this may be so, the present study indicates that minor factors can be important once the major factor for resistance is rendered ineffective. Gabo carries one minor factor, tentatively designated Sr_{G1}, for resistance to Australian field strains. This factor gives a " 3 — c " type of reaction in the seedling stage. Charter and Yalta do not possess this minor factor, but it is present in Bobin 39 and Gular.

To strain 103–H–2, seedling resistance of Gabo was governed by a single factor, Sr_{G2}, which is distinct from the two previously mentioned factors in this variety. Sr_{G2} is also present in Charter, but not in Yalta. Whether Sr_{G2} is identical with one of the two factors for resistance found in Gabo by Athwal (1953) cannot be ascertained as Athwal used Indian race 42, as mentioned earlier.

When strain A20 of *P. graminis* var. *secalis* was employed, a fourth factor for resistance, Sr_{G3}, was found in Gabo and this factor was also present in Charter but not in Yalta. Thus, when testing with strains 126–Anz–6, 103–H–2 and A20, no segregation for susceptibility occurs in crosses between Gabo and Charter, but this is in each case due to a different resistance factor. The type of seedling reaction of Gabo and Charter to these three strains, however, is very similar. Yalta carries only Sr11 and is susceptible in the seedling stage to 103–H–2 and A20.

Results on the resistance of Kenya 117A in the seedling and adult plant stage are in agreement with those reported by earlier investigators (Watson and Waterhouse, 1949 ; Athwal, 1953 ; Athwal and Watson, 1954 ; Knott and Anderson, 1956). During the present investigations it was found that the major gene for seedling resistance in Kenya 117A, Sr9b, was the same as that which gives resistance in the mature plant stage. The other two factors, presumably Sr7 and Sr10, had only a modifying influence under Australian field conditions. The modifying effect of these genes was evident when the field reactions of F_1 seedlings from crosses of Kenya 117A and Gamenya* with susceptible varieties were compared. Gamenya apparently carries the factors Sr9b and Sr_{G1} only, the latter factor derived from Gabo and having no influence on field reaction. Because Gamenya does not carry Sr7 or Sr10, F_1 seedlings from crosses with Gamenya are moderately susceptible in the field, while those from crosses with Kenya 117A are intermediate. It was also found that with most strains the genes of Kenya 117A were incompletely recessive in seedlings and in adult plants. The effect of these genes was additive rather than epistatic.

The three genes, when homozygous, produced different reaction types when tested with different strains. This result is in agreement with those of Green *et al.* (1960). Sr9b was very effective against strain 222–Anz–1, 2, 4, 6 at all temperatures, but lines carrying either Sr7 or Sr10 were moderately susceptible when tested with this strain. At temperatures of 65° to 70°F lines possessing Sr9b only were more resistant to 126–Anz–2, 6 than to 21–Anz–2 and NR–7, but became increasingly susceptible at higher temperatures. Lines which carried either Sr7 or Sr10 were more resistant to 21–Anz–2 than to 126–Anz–2, 6 and NR–7 to which they gave identical reaction types. The data suggested that Sr7 gives less protection than Sr10 under Australian conditions. Sr10 would be a valuable gene in combination with other genes, but it is ineffective on its own. As the seedling reaction produced by this

* Bred from a cross Gabo × [(Gabo^5 × Mentana) × (Gabo^2 × Kenya 117A)].

gene is easily discernible from a susceptible type there should be no difficulty in incorporating it into varieties. Although ineffective in adult plants in the field, and hence useless on its own for breeding, Sr10 is apparently operative in the seedling stage against all Australian strains of stem rust. Plants possessing Sr9b, by contrast, react differentially and are rendered ineffective by several strains now well established in the field, e.g., 17 — 2, 3, 21 — 2, 3, 21 — 1, 2, 3, 21 — 2, 3, 4, 21 — 2, 3, 6 and 116 — 2, 3 (Watson and Luig, 1963).

These studies further demonstrate that the strains of stem rust used in this study can be grouped as follows when plants having specific genes from Kenya 117A are inoculated with them:

Group I : 21–Anz–0, 21–Anz–2, 21–Anz–2, 6
Group II : 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6
Group III : 222–Anz–1, 2, 4, 6
Group IV : NR–7
Group V : 21–Anz–2, 3

The results from studies on the inheritance of resistance in Mentana to two strains of stem rust can be interpreted on the basis of two apparently independent factor pairs. Against most Australian field strains, like 21–Anz–2, a single factor, Sr8, conferred resistance in the seedling stage, this resistance being of a chlorotic " 2 — " reaction type. The same factor was operative against NR–7, but Mentana also possessed a second factor which conditioned a necrotic type " X = " reaction to this laboratory strain. The combined effect of these two factors, Sr8 and Sr_{M1}, was to make Mentana practically immune at low temperatures (" 0 ; " reaction type).

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